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ENERGY TRANSFER AND QUANTUM YIELD IN PHOTOSYSTEM II

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The photoreduction and dark reoxidation of Q_α and Q_β, the primary electron acceptors of Photosystems (PS) IIα and IIβ, respectively, in the presence of 3-(3′,4′-dichlorophenyl)-1,1-dimethylurea (DCMU) were studied in tobacco chloroplasts by means of fluorescence and absorbance measurements. The magnitude of a correction for an absorbance change by the oxidizing side of PS II needed in our previous study of the quantum yield of Q reduction (Biochim. Biophys. Acta 635 (1981), 111–120) has been determined. The absorbance change occurs in PS IIα mainly. The maximum fluorescence yield was found to be the same as in the mutant Su/su, which has a 3-fold higher reaction center concentration and a lower PS IIα to PS IIβ ratio. The kinetics of the light-induced fluorescence increase were measured after various pretreatments and the corresponding kinetics of the integrated fluorescence deficit were analyzed into their α and β components. From the results the contribution to the minimum fluorescence level, the degree of energy transfer between units, and the quantum efficiency of Q reduction were calculated for both types of PS II. This led to the following conclusions. The absence of energy between PS IIβ antennae is confirmed. Fluorescence quenching in PS IIα was adequately described by the matrix model, except for a decrease in the energy transfer between units during photoreduction of Q_α, possibly due to the formation of 'islets' of closed centers. PS II reaction centers in which Q is reduced do not significantly quench fluorescence. The ratio of variable to maximum fluorescence, 0.77 in PS IIα and 0.92 in PS IIβ, multiplied by the fraction of Q remaining in the reduced state after one saturating flash, 0.88 in PS IIα and greater than 0.95 in PS IIβ, leads to a net quantum efficiency of Q reduction in the presence of DCMU and NH_2OH of 0.68 in PS IIα and about 0.90 in PS IIβ. These values are in good agreement with the measured overall quantum efficiency of Q reduction.

Introduction

The chlorophyll fluorescence yield in chloroplasts may vary by more than a factor of five, depending primarily on the redox state of Q, the primary electron acceptor of PS II [1]. Other quenching processes being constant, the rate of PS II electron transport is proportional to the difference between the observed fluorescence yield and the maximum yield reached when all Q is reduced (reviewed in Ref. 2). Consequently, the kinetics of photoreduction of Q are conveniently measured by integration of this 'fluorescence deficit' during a so-called fluorescence induction curve. If no significant reoxidation of Q^- occurs (e.g., in the presence of DCMU), the observed reduction rate of Q then is proportional to light intensity, absorption cross-section or antenna size per PS II reaction center, and quantum efficiency of the process. The value of the integral of the fluorescence deficit obtained after complete photoreduction of Q, i.e., the size of the 'fluorescence induction area', is often used in comparative experiments as a measure of the total amount of photoreducible Q.

With homogeneous illumination, which in normal chloroplasts can only be obtained at wavelengths where the absorbance is low, the photoreduction of Q is usually biphasic, at least in higher plant chloro-

Abbreviations: Tricine, *N*-tris(hydroxymethyl)methylglycine; PS, photosystem; Chl, chlorophyll.

plasts. On this basis, Melis and Homann [3] postulated the existence of two types of PS II, which they called α (fast phase) and β (slow phase). The excitation spectra of the two kinetic phases [4] show that different pigment antennae are involved. PS IIβ has exponential induction kinetics. In mature normal chloroplasts in the presence of divalent cations at physiological temperatures, the fluorescence of PS IIα has strongly sigmoidal induction kinetics: the rate constant of Q_α reduction increases about 3-fold during the induction. This phenomenon can be ascribed to excitation transfer between PS IIα units, but the probability of transfer given by Melis and co-workers [5,6] was lower than that predicted from a matrix model, in contrast to data obtained by others [7,8]. The photochemical reactions in the two systems are probably the same [5,6], but secondary electron transport at the reducing side differs markedly [9, 10].

We have reported previously [11] that the quantum efficiency of Q photorereduction, under optimal conditions, is the same in PS IIα and PS IIβ. A net value of 1.0 was obtained and the apparent inconsistency of this outcome with the known occurrence of losses, such as fluorescence emission, was ascribed to an overestimation of the concentration of Q: [Q] was determined from the light-induced absorption increase at 325 nm and no correction was made for the absorption increase caused by the concomitant oxidation of an endogenous electron donor [12,13] because its amplitude was not known. A high quantum yield would justify the assumption of a significant fluorescence quenching by reaction centers in the state Q^- [14]. This assumption leads to important quantitative differences in the interpretation of the fluorescence induction curves.

These uncertainties prompted us to carry out a detailed quantitative study of fluorescence quenching by Q_α and Q_β and the quantum efficiency of their photoreduction.

Materials and Methods

Plants of tobacco (cv John William's Broadleaf) were cultured and chloroplasts were isolated as described in Ref. 11. Dark-adapted chloroplasts were suspended in isolation medium (50 mM Tricine, 0.4 M sucrose, 10 mM KCl and 5 mM $MgCl_2$, pH 7.8) at a chlorophyll concentration of 50 μM, determined according to the method of Arnon [15]. The measurements were carried out at room temperature in the presence of 10 μM DCMU; further additions are indicated in the figure legends; NH_2OH, when used, was added just before measurement. Chl *a* fluorescence was measured at 685 nm with a bandwidth of 10 nm. The excitation light, which was strong enough to reduce all Q within 2 s, was filtered by the combination of Calflex C, Corning CS 4-96 and CS 3-67 filters transmitting from 550 to 600 nm. Absorbance changes were measured as described before [11].

Results

Initial illumination of dark-adapted chloroplasts causes an absorbance increase in the near ultraviolet due to the oxidation of an endogenous electron donor of PS II [12,13]. The artificial electron donor NH_2OH prevents this absorbance change, does not absorb in this wavelength region and is oxidized by PS II to molecular nitrogen [16], leading, in the presence of DCMU, to a virtually irreversible photoreduction of Q.

The contribution by the oxidation of cytochrome *f* and *P*-700 to the measurement of the absorbance change at 325 nm (ΔA_{325}) in the presence of NH_2OH was determined in a second illumination, after rereduction of cytochrome *f* and *P*-700 (Table I). After subtraction of this contribution and correction for reduction of about 15% of Q_α upon addition of DCMU by the reduced secondary acceptor [9], we find a ΔA_{325} of $1.2 \cdot 10^{-4}$ corresponding to reduction of all Q. With ferricyanide present instead of NH_2OH, as in Ref. 11, Q and cytochrome *f* were completely oxidized before illumination and photooxidation of *P*-700 did not contribute a significant change at 325 nm [17]; reduction of Q and oxidation of the donor caused an absorbance change of $1.7 \cdot 10^{-4}$. Hence, under this condition, Q reduction contributed 70% to the absorbance change at 325 nm, which implies that the quantum yield of Q reduction was only 0.7-times the value reported previously [11].

As evidenced by the absorbance change due to reduction of Q, the total PS II reaction center concentration was almost 3-times higher in chloroplasts of the mutant Su/su than in the wild type. In this mu-

TABLE I

THE ABSORBANCE CHANGE AT 325 nm

The light-induced absorbance changes at 325, 420 and 700 nm were measured in the presence of 10 μM DCMU, gramicidin D and ferricyanide or NH_2OH, with an optical pathlength of 0.12 cm. The results shown were not corrected for particle flattening. ΔA_{700} was caused by oxidation of P-700, ΔA_{420} by oxidation of *P*-700 and cytochrome *f*. In the presence of ferricyanide ΔA_{325} mainly reflected the oxidation of an endogenous donor of PS II and the reduction of Q; in the presence of NH_2OH ΔA_{325} is due to the reduction of Q and the oxidation of cytochrome *f*, only the latter of which is reversible.

Additions	ΔA_{325} (X10⁴)	ΔA_{420} (X10⁴)	ΔA_{700} (X10⁴)
0.5 M ferricyanide	1.7	0.3	1.8
1 mM NH_2OH			
1st illumination	1.3	1.3	6.6
2nd illumination	0.2	1.2	6.3

tant 60% of the induction area was associated with PS IIβ and Q reduction accounted for 80% of the absorbance change measured in the absence of an artificial electron donor. Apparently, the absorbance change at 325 nm caused by the donor side originates in PS IIα mainly. The maximum fluorescence yield, ϕ_m, of the mutant chloroplasts, observed after complete photoreduction of Q and the plastoquinone pool, was within 5% the same as in the wild type. the fraction of chlorophyll in PS II was similar in both types of chloroplasts [11].

In the wild-type chloroplasts used in this study PS IIβ accounted for 14% of the variable fluorescence, F_v, and for 32% of the induction area, as shown in Fig. 1. As explained in the Introduction, the kinetics of the integrated fluorescence deficit represent the kinetics of Q reduction. Only a few points are shown, but in the integral a signal-to-noise ratio of 1000 is

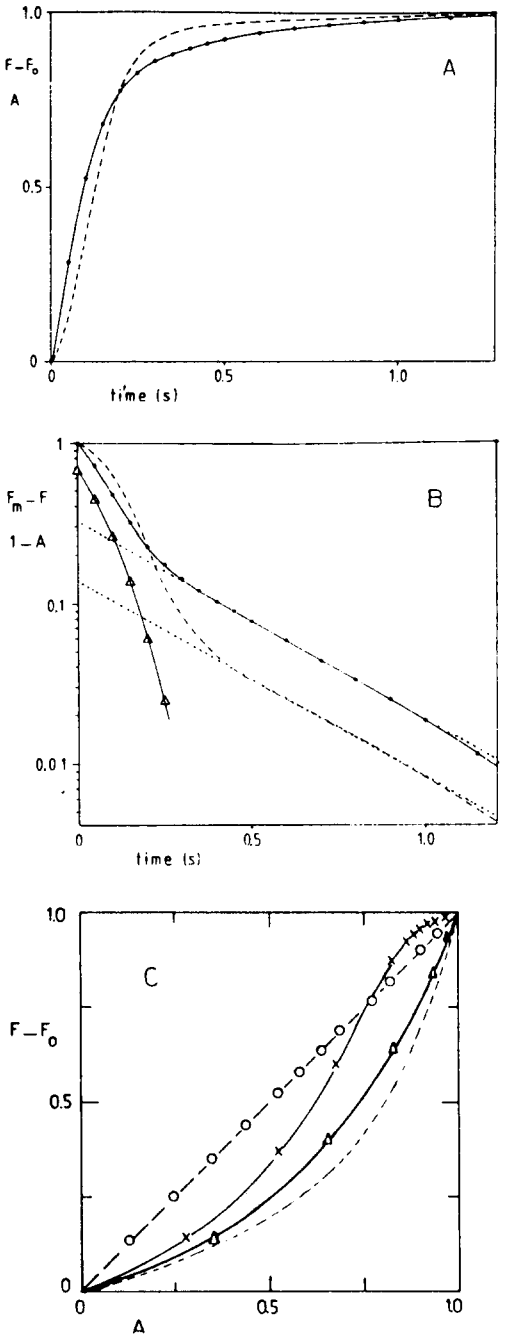

Fig. 1. (A) Time courses of the fluorescence increase induced by 550–600 nm light in the presence of 10 μM DCMU and 2 mM NH_2OH (------) and of the integrated fluorescence deficit, A (———). The F_m/F_0 ratio of these chloroplasts was 4.5. (B) Semilogarithmic plots of the fluorescence deficit ($F_m - F$) and its integral from the experiment of A. The exponential phase which had a rate constant of 2.9 s^{-1} (k_β) accounted for 14% of the variable fluorescence and comprised 32% of the induction area. (△———△) Kinetics of the fast phase of the integrated fluorescence deficit, obtained by subtraction of the slow phase. The initial rate constant ($k_{\alpha,i}$) was about 8.0 s^{-1}. (C) Relationship between fluorescence increase and induction area for the total induction curve (X———X), for PS IIβ (○———○) and for PS IIα (△———△). (------) The hyperbolic relationship predicted by the matrix model for PS IIα with an F_v/F_m ratio of 0.77 [18].

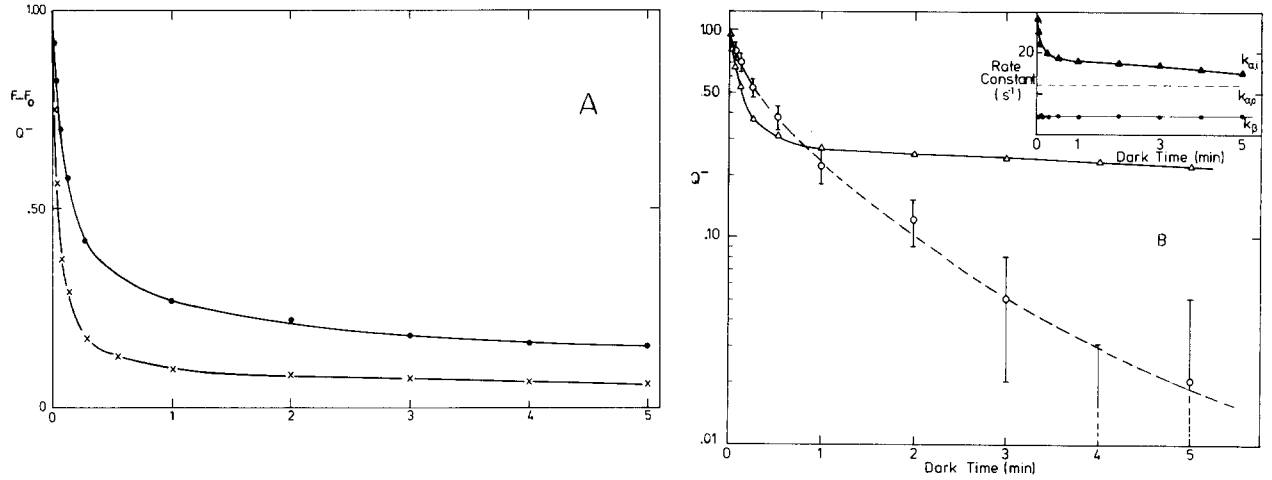

Fig. 2. (A) Decay of the initial fluorescence level (X———X) and of Q^- (●———●) after a short illumination in the presence of DCMU, which closed all the reaction centers. The chloroplasts used here had an F_m/F_0 ratio of 4.8. (B) Kinetics of reoxidation of Q_α^-(△, ▲) and Q_β^-(○, ●). The inset shows that the initial value of $k_\alpha(k_{\alpha,i}; k_{\alpha,0}$ is the initial value of k_α observed upon first illumination of dark-adapted chloroplasts) depended on the fraction of Q_α reduced, while k_β was invariant.

routinely obtained. After subtraction of the slow exponential phase due to Q_β reduction, the rate 'constant' of Q_α reduction is seen to grow from 2.8- to 8-times the rate constant of Q_β reduction. Correspondingly, a plot of the fluorescence increase vs. induction area (Fig. 1C) can be analyzed into a straight line for Q_β reduction and a strongly curved one for Q_α reduction, as in Ref. 6. Energy transfer between units, which may explain the kinetics of PS IIα, apparently does not occur in PS IIβ.

In Fig. 1 the artificial electron donor NH_2OH had been added. In its absence Q^- becomes reoxidized by a back reaction with an oxidized component at the donor side of the reaction center [19]. The reoxidation of Q^- after complete photoreduction in the presence of DCMU was studied by recording induction curves after increasing dark times. As Fig. 2 shows, complex kinetics were obtained, in agreement with Ref. 20. Most of Q_α^- was reoxidized with a half-time of 3 s; the remaining 30% decayed very slowly. The reoxidation of Q_β^- had more homogeneous, though nonexponential, kinetics with a half-time of about 20 s. Again the rate constant of Q_α photoreduction was dependent on the reduction level of Q_α, while that of Q_β was invariant (Fig. 2B, inset). As will be argued in the Discussion, the contributions of PS IIβ and PS I to the minimum fluorescence level, F_0, are negligible. From an analysis of the fluorescence rise kinetics we can then calculate the maximum

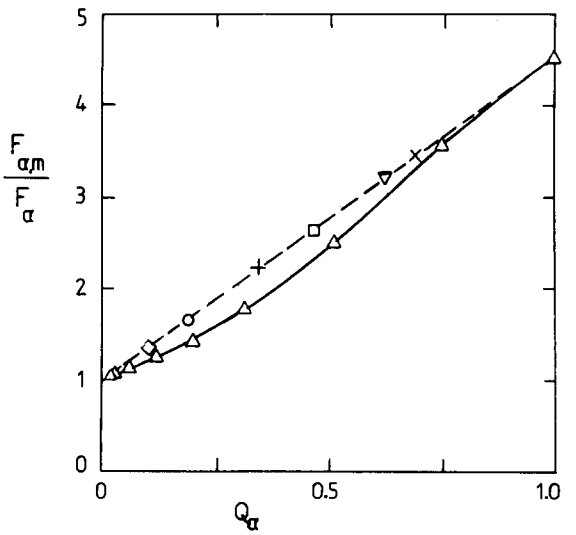

Fig. 3. Reciprocal fluorescence yield of PS IIα vs. oxidized fraction of Q_α. The points indicated by the triangles were obtained from an analysis of the induction curve recorded during first illumination of the chloroplasts used in the experiment of Fig. 2, in the presence of DCMU. The symbols on the straight line correspond to the initial fluorescence of PS IIα after (from left to right) 1, 2, 4, 8, 16 and 32 s of darkness after complete photoreduction (experiment of Fig. 2).

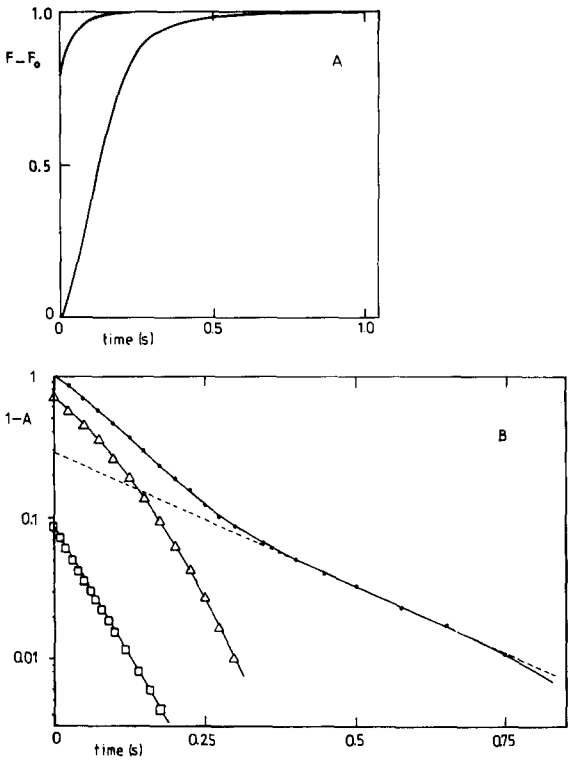

Fig. 4. (A) Time course of the fluorescence increase of chloroplasts in the presence of DCMU and NH_2OH; the F_m/F_0 ratio was 4.4. A saturating flash ($t_{1/2}$ = 3 μs) given 0.1 s before recording fluorescence (upper curve) left about 20% of the variable fluorescence and about 8% of the integrated fluorescence deficit. (B) Semilogarithmic plots of the induction area without (•) and with (□) saturating flash given before. The fast phase of the control curve (△) had an initial rate constant of 8.0 s^{-1} and a maximal rate constant of about 20 s^{-1}. After the flash remaining Q was reduced with a rate constant of about 18 s^{-1}.

fluorescence of PS IIα, $F_{\alpha,m}$, as well as F_α, the fluorescence attributable to this PS after different dark times. Fig. 3 shows that the fluorescence quenching by Q_α abeys the Stern-Volmer equation $F_{\alpha,m}/F_\alpha = k[Q_\alpha] + 1$ during reoxidation, whereas during photoreduction a significant deviation develops. This is also seen in Fig. 1C where the dashed line was calculated assuming linearity of $1/F_\alpha$ vs. $[Q_\alpha]$.

Even in the presence of DCMU and NH_2OH a short, saturating light flash does not reduce all Q (Fig. 4A). Presumably, a competition between back reaction and electron donation causes some losses shortly after the flash. A subsequently measured fluorescence induction curve revealed that about 12% of Q_α remained, while no significant amount, i.e., less than 5%, of Q_β could be detected (Fig. 4B). After two flashes the remaining fluorescence induction was too small for analysis; after three flashes it was undetectable.

Discussion

The quantitative interpretation of fluorescence induction curves in chloroplasts depends on the site of fluorescence quenching assumed to explain the fact that the maximum fluorescence yield is about 2.5-times lower than that of chlorophyll in solution, as may be estimated from the measured lifetime [21]. If this quenching occurs in the antenna it competes with photosynthesis. On the justifiable assumption that it affects the emission of all chlorophyll equally, the efficiency of excitation trapping by the photochemical reaction in PS II then is equal to F_v/F_m, normally close to 0.8. The efficiency of stabilization of the charge separation, taking the average flash yield from Fig. 4, is 0.9. Together these values predict a net quantum yield of Q reduction, in the presence of DCMU and NH_2OH, of 0.7, in good agreement with the value determined in this paper from the measurements of Q reduction rate and absorbed light intensity reported earlier [11].

Assuming a higher quantum yield of PS II, Duysens [14] proposed that the quenching process occurs in reaction centers in the state Q^-. When Q is in the oxidized state, the efficiency of the photochemical reaction may be 0.9, because the fluorescence yield is about 10-times lower than that of chlorophyll in solution. The net quantum yield of Q reduction should then be larger than 0.8. Unless the rate constants involved are very different, the quenching by reaction centers in the state Q^- would be stronger in PS IIβ than in PS IIα because the number of chlorophyll molecules per center is (about 3-times, see below) smaller in PS IIβ. Consequently, the ratio of PS IIα to PS IIβ is lower than the ratio of their contributions to the fluorescence induction area: in the chloroplasts used in the measurement of Fig. 1 the concentrations of Q_α and Q_β would be nearly equal, instead of 2 : 1. Because Q_β photoreduction is 3-times slower than Q_α photoreduction, the higher relative amount of Q_β would imply a lower value of the measured quantum yield of Q reduction. For the chloroplasts of Fig. 1 a

value of less than 0.6 was calculated, with an estimated uncertainty of 0.1.

Thus, our data not only remove the need to assume quenching by centers in the state Q^-, but also indicate that such quenching is insignificant. An independent check of the validity of Duysens' assumption would be to compare the relative amounts of Q_α and Q_β determined from absorbance changes and from fluorescence induction. Unfortunately, kinetic analysis of the absorbance changes of Q reduction, measured at 325 and 270 nm, failed to produce conclusive evidence, because a sufficient signal-to-noise ratio could not be reached (Van Gorkom, H.J. and Lelie, J.C., unpublished observations; see also Ref. 5). However, the observed proportionality between the fluorescence deficit and the rate of NH_2OH oxidation [22] shows that the relative amount of Q_β cannot be very different from its contribution to the induction area. Also, the absence of triplet formation in the PS II reaction centers in chloroplasts [23] argues against fluorescence quenching by reaction centers in the state Q^-, because the analogous process in bacterial photosynthesis proceeds via a recombination of the primary charge pair, P^+I^-, to the triplet state of P [24]. If the same process occurs in PS II we have to conclude that in chloroplasts at room temperature its quantitative importance is negligible for our purposes. Possibly the formation of P^+I^- is impeded by the presence of Q^-, or recombination to the singlet excited state of P is too rapid.

The conclusion reached above allows a more detailed interpretation of the fluorescence data. There is no evidence for a significant fluorescence emission by PS I near 685 nm at room temperature. For PS IIα and PS IIβ, both at F_m and at F_0, the fluorescence yield is determined by the equation

$$\Phi = \frac{k_f}{k_f + k_1 + k_q \cdot [Q]/[Chl]} \tag{1}$$

in which k_f and k_1 are the rate constants of deexcitation via fluorescence and via other loss processes in the antenna, including the quenching discused above. Since the maximum fluorescence yield was the same in a mutant with very different relative amounts of PS IIα and PS IIβ, the values of k_f and k_1 are probable the same in the two types of PS II antennae. If we assume that also the rate constant of deexcitation via Q photoreduction, k_q, is equal in the PS IIα and IIβ, the contributions of both systems to F_0 can be calculated. At the F_0 level, when all Q is oxidized, [Q]/[Chl] is equal to $1/N$, N being the average number of chlorophyll molecules per reaction center, which is larger in PS IIα than in PS IIβ. From eqn. 1 it follows that:

$$\frac{F_m}{F_0} = 1 + \frac{k_q}{k_f + k_1} \cdot \frac{1}{N},$$

or

$$F_0 = \frac{k_f + k_1}{k_q} \cdot N \cdot (F_m - F_0) \tag{2}$$

and hence, if R denotes the ratio $\alpha : \beta$ for the property indicated by a suffix,

$$R_{F_0} = R_N \cdot R_{F_v} \tag{3}$$

The value of R_N may be calculated from the ratio R_k of the observed rate constants $k_{\alpha,i}$ and k_β of Q photoreduction (Fig. 1) after correction for the different trapping efficiencies given by F_v/F_m and for the different efficiencies of charge stabilization in the two systems given by the yield, y, in a saturating flash (Fig. 4):

$$R_N = \frac{R_k}{R_y} \cdot \frac{R_{F_m}}{R_{F_v}} \tag{4}$$

Thus, one obtains a quadratic equation in R_{F_0} which can be solved:

$$R_{F_0} = \frac{R_k}{R_y} \cdot R_{F_m}$$

$$= \frac{R_k}{R_y} \cdot \frac{F_{\alpha,v} + F_0 \cdot R_{F_0}/(R_{F_0} + 1)}{F_{\beta,v} + F_0/(R_{F_0} + 1)} \tag{5}$$

For the chloroplasts used in Figs. 2 and 3 a value of 21 was obtained, so that 95% of F_0 was due to PS IIα.

This outcome was used in the construction of Fig. 3, but only a value of less than 80% would cause a significant nonlinearity of $1/F_\alpha$ vs. the concentration of oxidized Q_α at different dark times after complete photoreduction. A linear relationship between $1/F$

and quencher concentration was demonstrated earlier for the fluorescence quenching by dinitrobenzene in aerobic *chlorella* [7], in which no PS IIβ seems to occur, and during photoreduction of Q in Tris-washed spinach chloroplasts in the presence of DCMU [8], which revealed no fluorescence increase of PS IIβ.

The linearity of $1/F$ vs. [Q] not only shows that there is no significant barrier to excitation transfer between PS IIα units, in addition, it implies, according to model calculations (Van Grondelle, R., unpublished results), that on the average each excitation visits a reaction center pigment more than once before it is trapped. This finding is relevant for quantitative studies on delayed fluorescence; the emission yield for excitations originating by charge recombination in a PS IIα reaction center should be close to ϕ_0 when all Q_α is oxidized and should depend to some extent on the redox state of Q_α in the neighboring centers, as observed by Malkin and Barber [25].

During photoreduction of Q_α excitation transfer between PS II_α antennae seemed to decrease (Fig. 3, triangles). Possibly this is due to the formation of islets of closed units which results from the fact that a closed center enhances the absorption cross-section of Q_α reduction in its neighbors [26].

The net quantum yields of Q_α and Q_β reduction can now be calculated separately. In PS IIα a value of 0.77 for F_v/F_m, and of 0.88 for y indicate a net quantum yield of 0.68; in PS IIβ F_v/F_m was 0.92 and y was >0.95, indicating a net yield of about 0.90. Assuming a high efficiency for PS I, we calculated from the rate constants and the absorbed light intensity as in Ref. 11 that in the wild-type chloroplasts used in this study the antenna sizes were 200 chlorophyll molecules for PS I, 100 for PS IIβ and, when all Q_α was oxidized, 350 for PS IIα. Taking into account the proper corrections (see Table I), we found 2.3 Q per 1 000 chlorophyll molecules, together with 2.0 *P*-700, measured as described in Ref. 11, and 0.4 cytochrome *f*, estimated from both the light-induced absorbance change at 420 nm and from a chemically induced difference spectrum [27,28]. Since the losses in a saturating flash are presumably due to a back reaction of Q^- which proceeds for at most a few percent via decay of reexcited chlorophyll [29], the smaller flash yield of Q_α^- implies that the relative amount of Q_α is somewhat smaller than suggested by its contribution to the induction area. The resulting concentrations are 1.5 Q_α and 0.8 Q_β per 1 000 chlorophyll molecules.

The absorbance change caused by the donor side of PS IIα is probably associated with the $S_1 \rightarrow S_2$ transition only [13]. If it did not occur in PS IIβ its differential extinction coefficient was about 8 $mM^{-1} \cdot cm^{-1}$, or correspondingly higher if only part of the α centers were involved (cf. Fig. 2). It is possible that PS IIβ is mainly in the state S_0 after dark adaptation; simulation of the S-sate oscillation of PS IIα [9] required the assumption of a much lower initial S_0/S_1 ratio than indicated by oscillation patterns of oxygen evolution. Also, the absence of a slow phase in the decay of Q_β^- (Fig. 2) is noteworthy in this respect. The amplitude of the slow phase in Q_α^- reoxidation wax increased by very long dark adaptation and may result from electron donation by the component responsible for ESR signal II_s, which is oxidized by S_2 but not by S_1 [30]. Different deactivation kinetics of the S-states in PS IIβ may be expected in view of the different electron-transport properties at the acceptor side [9,10].

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References

1 Duysens, L.N.M. and Sweers, H.E. (1963) in Studies on Microalgae and Photosynthetic Bacteria (Japanese Society of Plant Physiologists, eds.), pp. 353–372, University of Tokyo Press, Tokyo
2 Lavorel, J. and Etiene, A.-L. (1977) in Primary Processes of Photosynthesis (Barber, J., ed.), pp. 203–268, Elsevier, Amsterdam
3 Melis, A. and Homann, P.H. (1975) Photochem. Photobiol. 21, 431–437
4 Thielen, A.P.G.M., Van Gorkom, H.J. and Rijgersberg, C.P. (1981) Biochim. Biophys. Acta 635, 121–131
5 Melis, A. and Duysens, L.N.M. (1979) Photochem. Photobiol. 29, 373–382
6 Melis, A. and Schreiber, U. (1979) Biochim. Biophys. Acta 547, 47–57
7 Sonneveld, A., Rademaker, H. and Duysens, L.N.M. (1980) Biochim. Biophys. Acta 593, 272–289

8 Van Gorkom. H.J., Pulles, M.P.J. and Etienne, A.-L. (1978) in Photosynthetic Oxygen Evolution (Metzner, H., ed.), pp. 135–145, Academic Press, London
9 Van Gorkom, H.J., Thielen, A.P.G.M. and Gorren, A.C.F. (1981) in Quinones in Energy Conserving Systems (Trumpower, B.L., ed.), Academic Press, New York, in the press
10 Thielen, A.P.G.M. and Van Gorkom, H.J. (1981) FEBS Lett. 129, 205–209
11 Thielen, A.P.G.M. and Van Gorkom, H.J. (1981) Biochim. Biophys. Acta 635, 111–120
12 Pulles, M.P.J., Van Gorkom, H.J. and Willemsen, J.G. (1976) Biochim. Biophys. Acta 449, 536–540
13 Velthuys, B.R. (1981) in Proceedings of the 5th International Congress on Photosynthesis (Akoyunoglou, G., ed.), International Science Services, Jerusalem, in the press
14 Duysens, L.N.M. (1979) in Chlorophyll Organization and Energy Transfer in Photosynthesis. The Ciba Foundation Symposium 61 (new series), pp. 323–340, Elsevier/North-Holland, Amsterdam
15 Arnon, D.I. (1949) Plant Physiol. 24, 1–15
16 Radmer, R. (1979) Biochim. Biophys. Acta 546, 418–425
17 Ke, B. (1972) Arch. Biochem. Biophys. 152, 70–77
18 Paillotin, G. (1976) J. Theor. Biol. 58, 237–252
19 Bennoun, P. (1970) Biochim. Biophys. Acta 216, 357–363
20 Melis, A. and Homann, P.H. (1976) Photochem. Photobiol. 23, 343–350
21 Porter, G., Synowiec, J.A. and Tredwell, C.J. (1977) Biochim. Biophys. Acta 459, 329–336
22 Bennoun, P. and Li, Y.-S. (1973) Biochim. Biophys. Acta 292, 162–168
23 Kramer, H.J.M. and Mathis, P. (1980) Biochim. Biophys. Acta 593, 319–329
24 Van Grondelle, R., Holmes, N.G., Rademaker, H. and Duysens, L.N.M. (1978) Biochim. Biophys. Acta 503, 10–25
25 Malkin, S. and Barber, J. (1978) Biochim. Biophys. Acta 502, 524–541
26 Lavorel, J. and Joliot, P. (1972) Biophys. J. 12, 815–831
27 Davenport, H.E. (1972) in Proceedings of the 2nd International Congress on Photosynthesis (Forti, G., Avron, M. and Melandri, A., eds.), pp. 1593–1601, Dr. W. Junk, The Hague
28 Henningsen, K.W. and Boardman, N.K. (1973) Plant Physiol. 51, 1117–1126
29 De Grooth, B.G. and Van Gorkom, H.J. (1981) Biochim. Biophys. Acta 635, 445–456
30 Babcock, G.T. and Sauer, K. (1973) Biochim. Biophys. Acta 325, 483–503